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Research Article

The co-existence patterns between native and an invasive mosquito species in Hungary based on a field survey

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Abstract

Biological invasions by non-native mosquito species pose significant global economic and public health threats due to their high vector competence. Still, their ecological relationships with the native fauna are rarely considered. This field study investigates the association between *Aedes albopictus* and the native mosquito community in Hungary. We conducted field sampling from 2020 to 2023, identified 104,612 mosquitoes from 29 species captured in traps across 532 locations, and characterized species diversity as well as the abundance of native species at each trapping event. We found that, where *Ae. albopictus* is already present, its abundance was positively associated with the species richness and diversity of native mosquitoes even after controlling for spatial and seasonal effects. We identified several significant pair-wise associations between *Ae. albopictus* and native species, both in positive and negative directions. These correlative patterns may indicate either direct interaction between species (e.g., competition) or patterns of co-existence that are driven by a third variable in the background. We performed path analyses to uncover the causal relationship among environmental traits (temperature, precipitation, urbanization and distance from water surfaces), the abundance of *Ae. albopictus* and that of four native species depicting co-existence patterns with the invasive one. These analyses revealed that the co-occurrences of *Ae. albopictus* with *Anopheles plumbeus* and *Coquillettidia richiardii* were mediated by seasonal activity, indicating that invasive mosquitoes can thrive in ecological conditions that disfavor native species. However, path models for *Ochlerotatus dorsalis* and *Oc. geniculatus* suggested a more direct causal relationship with *Ae. albopictus*. Although we cannot exclude that interspecific competition may partly shape the distribution of invasive and native mosquitoes, environmental filtering via shared ecological preferences appears to play a dominant role in structuring co-occurrence patterns.

Key words: *Aedes albopictus*, BG-Sentinel mosquito trap, competitive exclusion, ecological niche, emerging infectious diseases

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Introduction

Biological invasion refers to the process by which non-native species spread into new environments and establish populations, and often has significant ecological, economic, and social impacts (Simberloff et al. 2013). Human activities, such as trade and travel, play an important role in introducing and spreading non-native species worldwide. Invasive species significantly alter ecological interactions by

competing with natives for resources, disrupting food webs, modifying habitats, transmitting diseases, and causing genetic changes through hybridization (McMichael and Bouma 2000; Richardson 2011; Pyšek et al. 2012). Therefore, invasive species exert their influence on other native species and ecosystems primarily through their biotic interactions, which encompass predation, parasitism, interspecific competition, and ecosystem engineering. These impacts can lead to declines in native species, ecosystem instability, and a reduction in ecosystem services crucial for human well-being. Understanding the impact of invasive species is vital to preserve native biodiversity and ecosystem functioning.

An increasing number of invasive mosquito species have appeared in Europe, posing substantial and immediate risks to public health and ecosystems, with *Aedes albopictus* being the most abundant and threatening (Medlock et al. 2015). The establishment and expected drastic expansion of this invasive mosquito in Europe (Carlassara et al. 2024) raises urgent concerns due to their ability to transmit various pathogens, such as viruses causing chikungunya, Zika fever, yellow fever, West Nile fever, Eastern equine encephalitis, La Crosse encephalitis, St. Louis encephalitis, Japanese encephalitis, or Rift Valley fever (Hubálek 2008; Medlock et al. 2012). Mosquito-borne diseases can significantly impact human populations, ranging from mild symptoms to severe illness and even death. Furthermore, the presence of invasive mosquito species could also disrupt local ecosystems and native species interactions, but these ecological impacts are generally less studied than the epidemiological consequences (Juliano and Lounibos 2005).

Theories about the ecological interactions of invasive species often emphasize that competition plays a pivotal role in shaping species assemblages, particularly when invasive species exploit similar resources and habitats as native species. One classic outcome of such competition is the competitive exclusion principle, which states that two species competing for the same limiting resources cannot stably coexist in the same ecological niche (Hardin 1960). In such cases, one species typically outcompetes and displaces the other, leading to a negative association between the abundance or presence of the competing species (Juliano and Lounibos 2005). However, coexistence may still emerge when species exhibit niche partitioning, whereby differences in behavior, temporal activity, habitat use, or resource preference reduce the intensity of direct competition (Schoener 1974; Chesson 2000). Niche partitioning allows for overlapping geographic distributions without direct competitive displacement. In relation to invasive mosquitoes, most available studies suggest that these species can occasionally have neutral or even positive effects on native or co-occurring species, while a few works indicate that they play a role in competition. For example, *Aedes japonicus* may enhance oviposition site attractiveness for *Culex pipiens*, thereby indirectly facilitating co-occurrence through behavioral cues (Kaufman et al. 2012). Similarly, the presence of multiple larval species, including *Ae. albopictus*, may dilute predation pressure on native mosquitoes, such as *Culex restuans*, leading to increased survival in shared habitats (Kesavaraju et al. 2007). In other cases, invasive species may modify the microbial community of breeding sites in ways that influence the growth or habitat selection of other species (Murrell and Juliano 2008). Nevertheless, some studies have demonstrated direct larval competition between invasive and native mosquitoes under controlled conditions (Juliano 1998; Juliano and Lounibos 2005), indicating that such interactions may occur under specific ecological contexts. These examples underscore that community

dynamics can also include indirect facilitative effects, and that not all outcomes of species introductions are necessarily antagonistic.

One of the most common approaches to infer ecological interactions between invasive and native species from field studies is the analysis of correlations in their prevalence or abundance across space and time. These co-occurrence patterns—whether positive or negative—are often used as proxies for making inferences about biotic relationships such as competition, facilitation, or neutral coexistence (Blanchet et al. 2020). However, observed co-occurrence patterns (either positive or negative) between invasive and native species in the field may also reflect shared habitat preferences or environmental filtering rather than biotic interactions. That is, species may co-occur simply because they are independently attracted to similar environmental conditions, such as urban habitats with artificial breeding sites or areas with suitable microclimates (Leibold et al. 2004; Götzenberger et al. 2012). In this context, habitat attraction or environmental affinity could lead to positive species associations, even in the absence of direct ecological interaction. Similarly, if species match their seasonal activity with the same environmental fluctuations, a positive association will exist between the abundance of these species across time (Blonder et al. 2014). On the other hand, a negative association between species' abundance can emerge in a given location without direct interaction between them if the species favor different ecological conditions. Accordingly, if species are attracted to different environmental optimum, they will be unlikely to be trapped at the same time or at the same location, which will lead to negative co-occurrences.

Studies, using field surveillance data, such as trap-based sampling across broad geographic scales, have shown that invasive *Aedes albopictus* often exhibits negative spatial associations with native species, such as *Culex pipiens*, *Ochlerotatus triseriatus*, and *Anopheles quadrimaculatus*, in parts of North America, suggesting the possibility of competitive exclusion (Benedict et al. 2007; Rochlin et al. 2013). However, other studies have found positive or neutral co-occurrence patterns depending on habitat type and environmental context (Leisnham and Juliano 2010), highlighting the complexity of inferring causality from field data alone. Numerous laboratory and field studies have demonstrated that interspecific competition, particularly among larval stages, could affect or play a significant role in shaping the outcomes of mosquito invasions (Juliano 1998; Braks et al. 2004; Juliano and Lounibos 2005; Kesavaraju et al. 2007). Experimental microcosms and field enclosures have repeatedly shown that the invasive *Aedes albopictus* is a superior competitor to both the invasive *Aedes aegypti* and the native North American *Ochlerotatus triseriatus*, often leading to reduced survival or displacement of the latter under resource-limited conditions (Teng and Apperson 2000). This competitive superiority has been attributed to more efficient resource utilization, insensitivity to inhibitory cues, and, in some cases, asymmetries in mating interference and egg hatching behavior. However, field observations also highlight that coexistence frequently occurs, suggesting condition-specific competition where abiotic factors (e.g., desiccation, temperature) or biotic interactions (e.g., predation, parasite escape) mitigate competitive exclusion. For instance, native predatory mosquitoes, such as *Wyeomyia* spp. or *Toxorhynchites* spp., may reduce the establishment success of *Ae. albopictus* in certain habitats. Overall, while larval competition is a central mechanism in mosquito invasions, its ecological impact is often context-dependent and modulated by broader environmental and community factors (Juliano and Lounibos 2005), while substantial evidence suggests facilitative effects on native species.

In this study, we investigate the ecological relationships between *Ae. albopictus* and native mosquito species using a large-scale field dataset collected across Hungary based on samples from adult traps. *Ae. albopictus* has been introduced in Hungary in the last 15 years (Soltész and Zöldi 2017; Sáringer-Kenyeres et al. 2020), and since then, they depicted a rapid spread (Garamszegi et al. 2023a; www.mosquitosurveillance.hu). We aim to evaluate whether the observed co-occurrence patterns among species are more consistent with direct competitive interaction or environmentally driven aggregation. Negative associations between species may point to competitive exclusion, particularly when species rely on similar larval habitats or resources and their spatial overlap is lower than expected by chance. However, environmentally driven aggregation may emerge if shared environmental preferences or activity patterns generate positive associations, even in the absence of direct biotic interaction. Such environmental mediators can also lead to negative associations between species if they differ in their ecological requirements. To investigate these possibilities, we apply path modeling to our field data collected over four years. The analyses incorporate climatic variables (temperature, precipitation), spatial and seasonal effects, and habitat characteristics (urbanization, proximity to water), allowing us to evaluate the relative contribution of interspecific interactions versus shared environmental responses in shaping mosquito community structure and to test inferences about the causal mechanisms.

Materials and methods

Direct field sampling

We conducted direct field sampling, collecting mosquitoes from 192 settlements and 532 locations during 897 trapping days between 2020 and 2023 (Fig. 1). To ensure national coverage, we selected at least seven settlements randomly from each county using a stratified random sampling method. These short-term traps were operated at each location for a minimum of 24 hours and a maximum of 5 days; however, in most cases, these traps were typically positioned for 2 consecutive nights at a sampling session. We also included 4 long-term traps (Budapest, Debrecen, Vác, Vácrátót) that operated permanently from May to October each year from 2021 and were checked daily. Short-term and long-term traps were purposefully positioned in areas with supposedly high mosquito activity, such as near water bodies and in urban areas. We used a standardized protocol for trap operation and mosquito collection, ensuring the reliability and comparability of our data.

BG-Sentinel mosquito traps were used with CO_2 and lure as attractants for mosquito sampling. The content of the traps was collected and stored in a freezer (-20 °C) until further examination, upon which all specimens were identified at the species level under a microscope by the same expert taxonomist based on morphological characteristics (Kenyeres and Tóth 2008; Briët et al. 2021). The specimens have been sexed based on their morphology, but for the current study, counts for females and males were combined. During the identification procedure, the list of species and the abundance of each species (i.e., the number of individuals) were determined for each trap (see Table 1 for descriptive statistics). The comprehensive and systematic approach for trapping and identification allowed us to gather a large dataset, providing a robust basis for our analysis and conclusions.

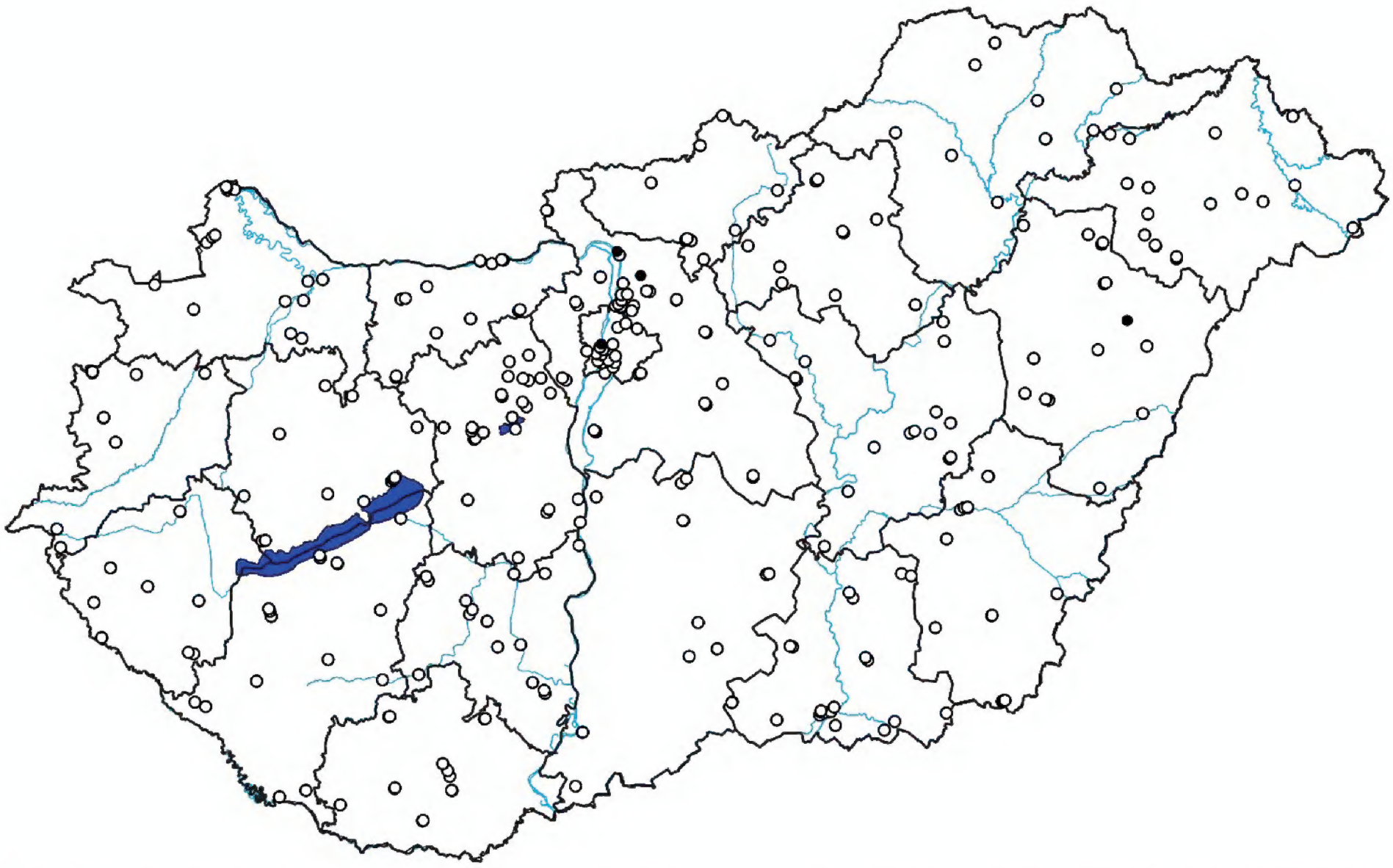

Figure 1. The localities that were selected to sample mosquito communities by using adult mosquito traps in the field in Hungary. The traps were operating at least for one night. The filled dots represent the permanent traps (operating continuously for several months), while the open dots indicate the short-term traps (operating temporarily for a few days only).

Importantly, we used identical BG-Sentinel traps with the same CO_2 and lure configuration at each location, thereby ensuring methodological uniformity; thus, we compare the composition of mosquito communities as referred from the trap samples across sites with different abundances of invasive mosquitoes.

Climate data

Georeferenced climatic data were gathered for each sampling location using the Hungarian Meteorological Service (HungaroMet) open Meteorological Database (odp.met.hu). The meteorological data were generated by MISH interpolation methods from the measured and quality-controlled, homogenized, and completed data (grid resolution: 10 × 10 km; see for more details: Szentimrey et al. 2005; Izsák 2023). We gathered site-specific temperature (daily average, in °C with 0.01 accuracy) and precipitation (daily sum, in mm with 0.01 accuracy) data from 30 days preceding the trapping date in the respective year.

Urbanization index

Based on the geographic coordinates of each sampling site, we calculated the urbanization index within the surrounding area (i.e., 1 × 1 km square). For this purpose, we used the 'UrbanizationScore' software (Czúni et al. 2012) that scores the abundance of vegetation, buildings and paved roads based on the corresponding aerial images from Google Maps. The program then combines this information into a principal component that arranges the study sites along an urbanization gradient.

Table 1. The number of individuals of mosquito species trapped between 2020 and 2023, and the number of settlements and traps where each species was captured within the short-term trapping campaign. For the long-term trapping campaign performed at four locations, only the total number of individuals captured for each species is shown. The scientific names of mosquitoes are written based on Snow and Ramsdale (2003). * Indicates invasive species, for which data were not used in this study.

	SHORT-TERM TRAPS					PERMANENT TRAPS
	specimens	**settlement**	**settlement %**	**trap**	**trap%**	**specimens**
Aedes albopictus	853	26	13.54	96	18.05	9040
Aedes cinereus	0	0	0	0	0	2
*Aedes japonicus**	38	16	8.33	19	3.57	10
*Aedes koreicus**	325	58	30.21	95	17.86	324
Aedes rossicus	0	0	0	0	0	2
Aedes vexans	3860	104	54.17	196	36.84	1097
Anopheles claviger	4	4	2.08	4	0.75	25
Anopheles hyrcanus	34	11	5.73	11	2.07	0
Anopheles maculipennis s.l.	62	16	8.33	21	3.95	22
Anopheles plumbeus	102	29	15.1	38	7.14	506
Coquillettidia buxtoni	1	1	0.52	1	0.19	5
Coquillettidia richiardii	476	25	13.02	39	7.33	289
Culex hortensis	0	0	1.56	0	0	14
Culex martinii	1	1	0.52	1	0.19	0
Culex modestus	80	21	10.94	26	4.89	75
Culex pipiens s.l.	42140	188	97.92	498	93.61	43437
Culiseta annulata	199	39	20.31	49	9.21	20
Culiseta longiareolata	27	10	5.21	15	2.82	0
Ochlerotatus annulipes	2	2	1.04	15	2.82	189
Ochlerotatus caspius	679	54	28.13	72	13.53	110
Ochlerotatus cataphylla	0	0	0	0	0	3
Ochlerotatus detritus	0	0	0	0	0	1
Ochlerotatus dorsalis	2	1	0.52	2	0.38	50
Ochlerotatus geniculatus	18	13	6.77	15	2.82	269
Ochlerotatus pulcritarsis	4	4	2.08	2	0.38	8
Ochlerotatus pullatus	0	0	0	0	0	28
Ochlerotatus sticticus	0	0	0	0	0	172
Ochlerotatus punctor	0	0	0	0	0	2
Uranotaenia unguiculata	4	4	2.08	4	0.75	1
TOTAL	**48911**	**192**		**532**		**55701**

Proximity to water surface

Based on the geographical coordinates, we calculated the distance between each trap location and the nearest surface water body (river, stream, lake, or pond) using QGIS 3.28. Distances were measured as straight-line (Euclidean) distances based on a hydrographic layer, and were later used as environmental variables in the analysis. The distance from the closest water surface was estimated in meters and was $\log_{10}$-transformed for the statistical analyses.

Statistical analyses

From the trap samples, we calculated the following variables reflecting the composition of the mosquito fauna for each trap originating from the direct fieldwork, if at least one individual for any native species were caught: i) species richness of the native mosquito fauna, ii) Shannon index to characterize the diversity of the native mosquito fauna by considering their relative abundance. We also calculated the abundance of *Ae. albopictus* and each native species that was captured at least once in the traps. Abundance values were $\log_{10}$-transformed for the statistical analyses.

First, we tested for the relationship between the abundance of *Ae. albopictus* and estimates that reflect the composition of the native mosquito community. This was done by testing for the correlation of these variables, and also by constructing mixed-effects models with spatial correlation structure, in which species richness or diversity index was entered as the response variable. In each model, the focal predictor variable was the abundance of *Ae. albopictus* ($\log_{10}$-transformed), and we also included detection date (circular variable using the sine and cosine of the radians of the actual date to define seasonal rhythms) to account for temporal effects. Given that the data were geographically distributed, ecological conditions as well as the composition of the mosquito community could be more similar between closely situated sampling locations than between distantly positioned traps. Therefore, we defined an exponential spatial correlation structure for the residuals based on the geographical coordinates of the sampling sites. In this way, the pseudo-replication caused by the traps operating at the same locations between collection events was also considered. To control for temporal non-independence of data due to year effects (data from the same year may be more similar than from different years), we set the random effect term based on year as a categorical variable as a random effect. The spatial mixed-effects models were performed using the statistical package "nlme" (Pinheiro and Bates 2025) in the R statistical environment.

Second, we investigated if any relationships between particular pairs of species can be observed in the data. For this, we examined if detected co-existence patterns between pairs of species followed a random expectation or shifted towards a positive or negative direction. Accordingly, we counted the traps that successfully captured *Ae. albopictus* or the given native species being compared (i.e., we identified at least one individual in the content of the trap) – independently of each other. Based on these observed incidences, we separately generated random scenarios for the presence of the two species along the sampling localities. We repeated these simulations 1,000 times, and in each run, we recorded how often the two species appeared together in the same traps purely by chance. These estimates define the null distribution of their expected co-occurrence, which was used as a statistical reference against the observed number of instances when both species were captured in the same trap. An observed number of co-occurrences lower than the 2.5^{th} percentile of the generated random distribution indicates a negative association between the two species, whereas co-occurrences exceeding the 97.5^{th} percentile of the null distribution suggest a positive association.

Third, to investigate if the significant relationships between the presence of species are mediated by a third variable that reflects common environmental conditions or by direct interspecific interactions, we fitted path analysis models. More specifically, by using the R package "piecewiseSEM," (Lefcheck 2016), we applied a piecewise structural equation modelling approach to distinguish between direct and indirect pathways, thus to make inferences about the causal associations among temporal variation in

activity, environmental factors and the abundance of *Ae. albopictus* and native species. This analysis/approach relied on the following 3 hypotheses: i) environmental conditions determined by climate and habitat characteristics establish the ecological prerequisite for the population growth of *Ae. albopictus* (i.e., environmental variables directly affect the abundance of *Ae. albopictus*); ii) native mosquitoes are also sensitive to such environmental conditions, thus the same climatic and habitat variables determine the abundance of native mosquitoes; iii) the abundance of *Ae. albopictus* can also have a partial impact on the abundance of native mosquitoes if the introduction and spread of the invasive species directly interacts with native populations.

To fit models for the above hypotheses, we relied on linear mixed-effects models with gaussian error terms available in the package "nlme" (Pinheiro and Bates 2025) that allowed incorporating random effects as well as accounting for spatial autocorrelation embedded in the geo-referenced data. In the first model incorporating predictions for hypothesis i), the response variable was the abundance (log_{10}-transformed) of *Ae. albopictus*, and the predictor variables included detection date to reflect seasonal effects (we treated date as a circular variable by using the sine and cosine of the radians of the actual date) and the environmental variables such as temperature (daily temperature averaged over 30 days prior to trapping), precipitation (precipitation over 30 days prior to trapping, log_{10}-transformed), urbanization (urbanization score) and distance from water habitats (log_{10}-transformed). We also included the interaction between temperature and precipitation, because in hot weather, water surfaces evaporate faster, and also because the positive effect of temperature should be more robust when the optimal breeding habitats are available (i.e. there is some rain that fills the small containers). An exponential spatial correlation structure, based on the geographical coordinates of the traps, was used to account for the spatial autocorrelation of data, while the pseudoreplicative effect of within-year variations were handled by defining an appropriate random effect structure based on year categories. The other model incorporating predictions for hypotheses ii-iii) was fit for the abundance of the native species (log_{10}-transformed), and had a structure very similar to the above model; the only exception was that it also included the abundance of *Ae. albopictus* (log_{10}-transformed) as a predictor variable. Before fitting the structural equation model, structural equations were simplified based on a manual backward stepwise procedure, by which non-significant predictors were removed one by one. We expected that seasonal variations primarily impact temperature, that they also depict fluctuations on a short-term time scale, thus we specified correlated errors for detection date (the sine and cosine of the radians) and temperature. For the path analysis, we only considered species, for which the pair-wise analysis of associatedness indicated significant deviations either in the positive or negative direction, and the distribution of data allowed this complex modelling (i.e., we did not proceed with species, which were detected in very few or too many trap samples, as these would have caused highly unbalanced distributions).

Results

The composition of the native mosquito fauna

In the raw data, there was no significant association between the abundance of *Ae. albopictus* and species richness of the native mosquito fauna (r = 0.009, N = 1517, P = 0.738). A similar result was found for Shannon diversity index (r = 0.023, N = 1517, P = 0.367). However, when we only included sites where

the invasive species was present, these relationships were significant and positive (species richness: $r = 0.281$, $N = 350$, $P < 0.001$; diversity index: $r = 0.263$, $N = 350$, $P < 0.001$; Fig. 2). In addition, when we constructed a mixed effect model that appropriately accounted for the spatial and temporal structure of the data, we found that the abundance of *Ae. albopictus* was a significant predictor of the Shannon diversity index with a positive slope (Table 2).

The presence of native mosquito species

The co-occurrence of *Ae. albopictus* and *Anopheles plumbeus* was detected in 12 traps only. *Ae. albopictus* was present in 350 trap samples, while *An. plumbeus* was captured in 180 instances. We can generate a null-hypothesis from these observations in which we expect that both species will be present in 41–53 samples simply by chance with 95% confidence. The detected co-occurrence (12) of the two species was significantly lower than this random expectation (Table 3). Similar comparisons for other possible species pairs suggested that out of the 26 native mosquito species assessed, *Ae. albopictus* showed statistically significant associations with 11 species (based on random chance, we expected that 5% of the 26 relationships, i.e., 1–2 of them, would be significant).

Table 2. The results of mixed-effects models with spatially correlated random effects testing for the association between the abundance of *Aedes albopictus* and estimates of the composition of the native mosquito fauna, while holding spatial and temporal effects constant.

Species richness of the native mosquito fauna				
Fixed effects	**Estimate**	**S.E.**	**t-value**	***P***
Intercept	1.768	0.252	7.028	< 0.001
Abundance of *Ae. albopictus*	0.088	0.062	1.425	0.154
sin(date)	-0.372	0.059	-6.267	< 0.001
cos(date)	0.188	0.128	1.470	0.142
Random effects				
Variance parameters				
Year				0.192
Residual				1.442
Dimensions				
# of obs.				1517
# of groups				4
Shannon diversity index of the native mosquito fauna				
Fixed effects	**Estimate**	**S.E.**	**t-value**	***P***
Intercept	0.175	0.052	3.352	< 0.001
Abundance of *Ae. albopictus*	0.077	0.020	3.813	< 0.001
sin(date)	-0.032	0.015	-2.089	0.037
cos(date)	0.054	0.034	1.596	0.111
Random effects				
Variance parameters				
Year				0.006
Residual				0.146
Dimensions				
# of obs.				1517
# of groups				4

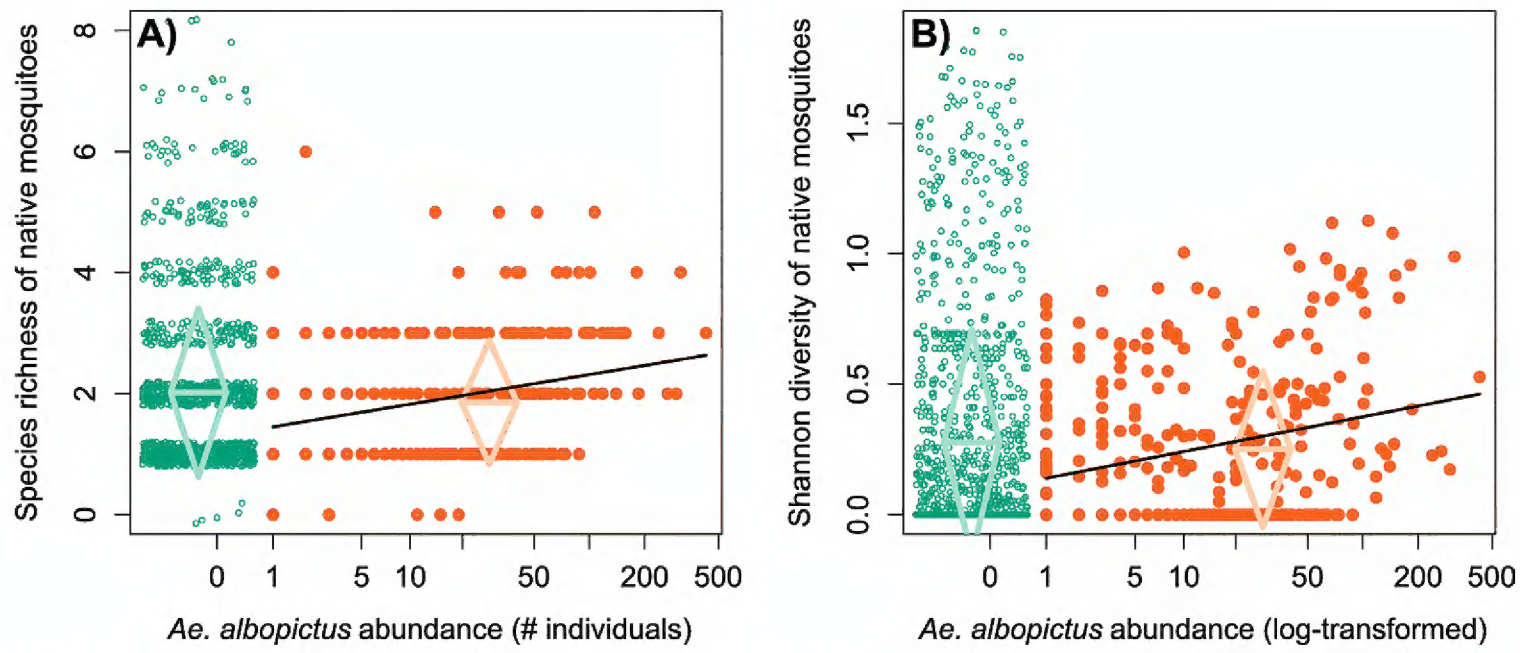

Figure 2. The relationship between the abundance of *Aedes albopictus* and species richness (**A**), species diversity (**B**) based on the content of traps originating from a direct field survey in Hungary. Colors (green and light brown) separate the data based on the presence or absence of the invasive species. Data are jittered for better visualization at zero prevalence of *Ae. albopictus*. The diamonds show the summary statistics (mean ± standard deviation) for the response variable when the focal invasive species is present or absent. The light brown lines show the regression lines that are fitted on the non-zero prevalence data (see Table 2 for the statistical models that take into account the potentially confounding effects of date, year, and spatial effects).

This includes positive associations (*Aedes cinereus*, *Ae. rossicus*, *Ochlerotatus dorsalis*, *Oc. geniculatus*, *Oc. pulcritarsis*) and negative associations (*Ae. sticticus*, *An. plumbeus*, *Oc. annulipes*, *Oc. detritus*, *Oc. pullatus*, *Cq. richiardii*).

The effect of environmental variables

The positive relationships between *Ae. albopictus* and native species may be mediated by environmental effects that render species pairs to be captured at the same time or location. In addition, such environmental effects may also raise negative associations between species, if they prefer very different ecological conditions, which results in rare co-occurrence patterns. We discriminated the direct and indirect causal effects of temporal fluctuations, environmental effects on the abundance of invasive and native mosquito species by using path analyses (Fig. 3). We performed such modelling for species, for which the distribution of data was the most balanced (e.g., for *An. plumbeus*, *Cq. richiardii*, *Oc. dorsalis* and *Oc. geniculatus* out of the 11 pairs of species with significant associations reflecting 2 positive and 2 negative associations, see Table 3).

Overall, the path models were statistically supported (*An. plumbeus*: Fisher's C_{10} = 8.500, P = 0.580; *Cq. richiardii*: Fisher's C_{10} = 8.149, P = 0.614; *Oc. dorsalis*: Fisher's C_2 = 1.186, P = 0.553; *Oc. geniculatus*: Fisher's C_{10} = 4.143, P = 0.941), and suggested the following general patterns: i) fine-scale variation in temperature is strongly determined by components of seasonality, ii) the abundance of *Ae. albopictus* primarily depends on the interaction between temperature and precipitation and urbanization (Fig. 4), while closeness to water habitats does not have such a mediator role. Models corresponding to different native species indicated that their abundance is dependent on seasonality (*An. plumbeus*, *Cq. richiardii*, *Oc. dorsalis*) and closeness to water habitats (*An. plumbeus*, *Cq. richiardii*, *Oc. dorsalis*, *Oc. geniculatus*). Temperature had also a significant path for *Oc. geniculatus*. Most importantly, there was no indication for direct relationship with the abundance of *Ae. albopictus* for *An. plumbeus* and *Cq. richiardii*. However, there was a significant path reflecting a positive causal relationship between the abundance of the invasive species and that of *Oc. dorsalis* and *Oc. geniculatus*.

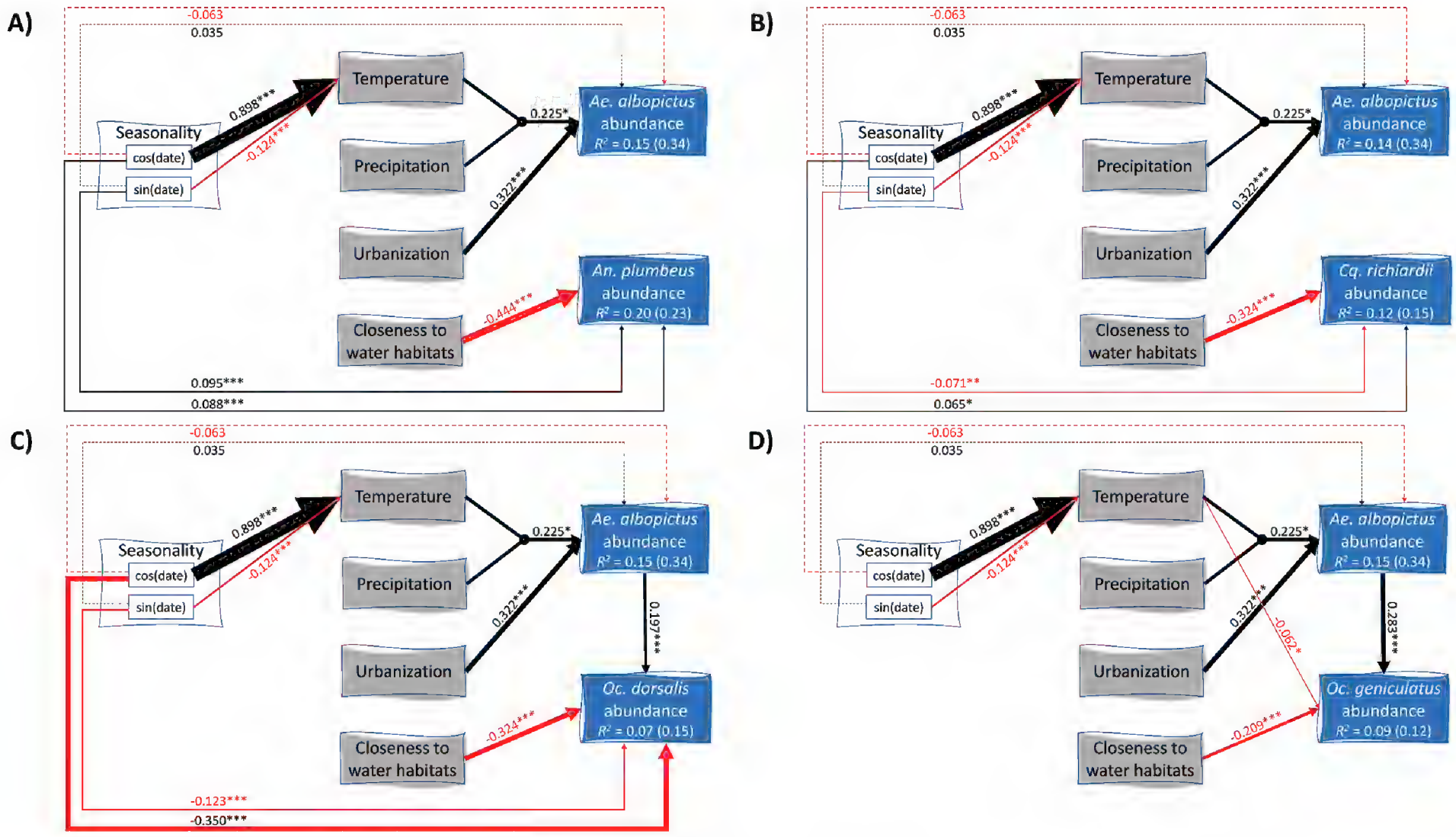

Figure 3. Path analyses unraveling the direct and indirect relationships between environmental variables and the abundance of *Ae. albopictus* and that of four native mosquito species with detected co-occurrence patterns (**A.** *An. plumbeus*; **B.** *Cq. richiardii*; **C.** *Oc. dorsalis*; **D.** *Oc. geniculatus*). The models included pathways that are defined by the underlying hypotheses (see main text). The final model includes all pathways after backward model simplification based on significance values. Variables describing within-year temporal fluctuations are in white boxes, grey boxes represent environmental variables, and measures of abundances are in blue boxes. Marginal (conditional) R-squared values for individual models are given with the corresponding response variables. Black arrows show positive effects, and red arrows show negative effects with a thickness that is proportional to the standardized path coefficient (which are also presented as values on the arrows). Node of two arrows indicates an interaction effect between the corresponding variables. Significance levels: *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$.

Discussion

The main results of this study were that i) the abundance of *Ae. albopictus* was positively associated with mosquito species richness and the diversity of the native mosquito fauna; ii) based on patterns of observed presence/absence of species in the traps, we detected evidence for significant positive co-occurrences for 3 species pairs and for significant negative co-occurrences for 8 species; iii) the abundance of *Ae. albopictus* was significantly associated with environmental variables (urbanization and the interaction between temperature and precipitation); iv) when we controlled for the potentially confounding effect of environmental variables, the positive relationship between the abundance of *Ae. albopictus* and that of 2 native mosquito species (*Oc. dorsalis* and *Oc. geniculatus*) were still significant.

The positive associations between the abundance of *Ae. albopictus* and species richness and diversity of the native mosquito fauna likely reflect shared environmental preferences rather than indicating facilitative biotic interactions. Most hypotheses about the effect of invasive species on native species emphasize the role of competition. Accordingly, competitive interactions among species should cause a negative relationship between the abundance of the invasive species and the diversity indices of the native community (e.g., Vilà et al. 2011; Mollot et al. 2017; Süle et al. 2023). However, while the population growth of an invasive species is unlikely to promote an increase in local species richness directly, it may, in some cases, contribute to

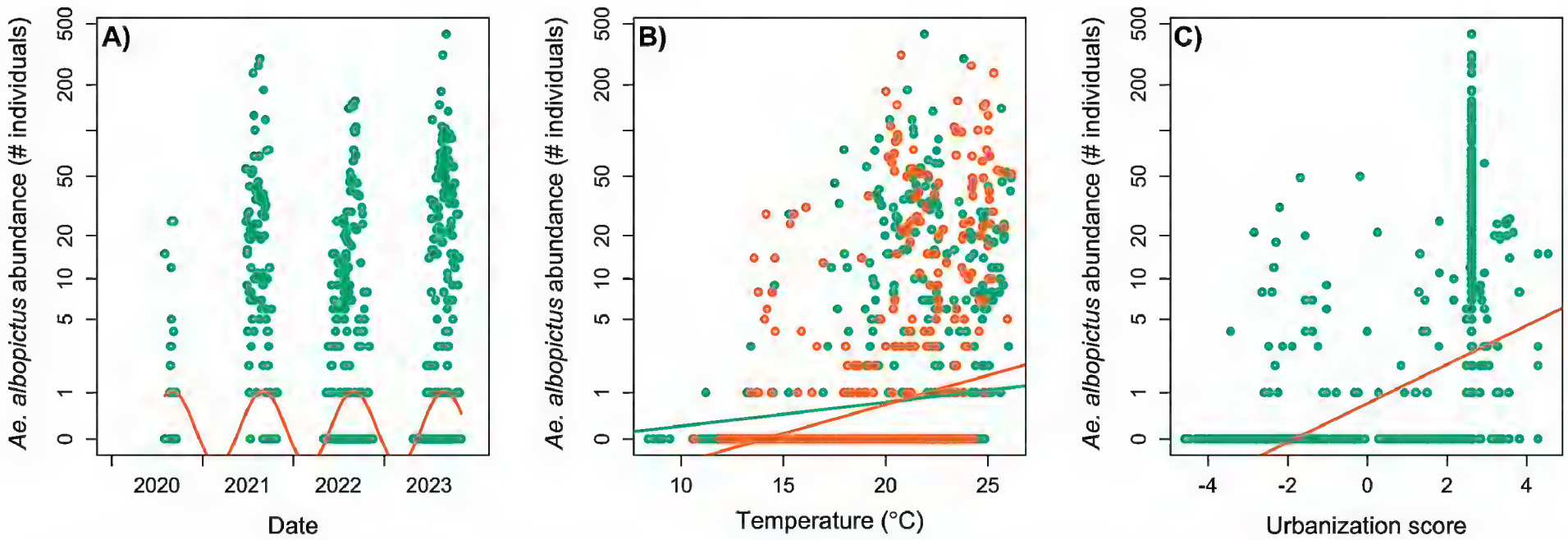

Figure 4. Effect of different environmental variables (**A.** Seasonality; **B.** The interacting effect of temperature and precipitation; **C.** Urbanization) on the abundance of *Ae. albopictus.* Dots represent trap samples, lines are regression lines. To demonstrate the interacting effect of temperature and precipitation (**B**), sites with different degree of rainfall are shown with different colors (green: precipitation during 30 days prior to trapping < 50 mm, brown: precipitation during 30 days prior to trapping >= 50 mm, as the 50 mm threshold is defined as the median of data distribution).

greater functional diversity, spatial heterogeneity, or the creation of novel ecological opportunities within communities via indirect effects (Pyšek et al. 2012; Schirmel et al. 2016). Therefore, it is more likely that *Ae. albopictus* tends to colonize sites that are already favorable for mosquitoes in general—such as warm, urbanized habitats with abundant container-type breeding sites—where overall mosquito abundance and diversity are naturally and inherently higher (Juliano and Lounibos 2005; Leisnham and Juliano 2012). Thus, the positive associations may emerge because *Ae. albopictus* is more likely to occur where environmental conditions support a rich native community, rather than because it enhances that diversity. This interpretation aligns with the idea that environmental filtering, rather than direct interactions, plays a key role in structuring mosquito assemblages at the landscape scale.

The co-occurrence analysis presented in this study demonstrates how diversity patterns of mosquito assemblages can be potentially influenced by interactions with particular species. By testing all possible invasive–native species pairs against null expectations, we were able to identify which particular associations may be responsible for the detected positive associations between the abundance of the invasive species and the diversity of the native mosquito community. Out of the 26 native species assessed, 11 showed statistically significant associations with *Ae. albopictus*, including both positive and negative relationships. This relatively high proportion suggests that co-occurrence with *Ae. albopictus* is not random and warrants further ecological interpretation. Patterns of co-occurrences have been reported in other regions as well. For instance, *Ae. albopictus* was found to co-occur with native *Ochlerotatus triseriatus* in the eastern United States, though laboratory studies indicated a competitive advantage of the invader (Livdahl and Willey 1991; Novak et al. 1993). In South America, *Ae. albopictus* and *Ae. aegypti* frequently co-occur, despite competitive interactions demonstrated under experimental conditions (Braks et al. 2003; Braks et al. 2004). These findings, together with our results, suggest that invasive *Ae. albopictus* can persist in communities with native mosquitoes. However, such co-occurrence patterns do not have implications about the potential causal effects of the invasive species on native ones: the co-occurrence patterns may be rather shaped by a combination of ecological overlap, environmental filtering, and potentially biotic interactions.

Table 3. The pairwise association between the presence of *Ae. albopictus* and the presence of native mosquitoes that were present at least in one trap during the course of the study. The results are based on simulations that estimate the expected number of co-occurrences of the two mosquitoes in the same trap given the number of instances when these species are caught. The significant associations are in bold, * indicate native species that were included in the path analysis.

Native species	# observed co-occurrence	The 95% CI range of the expected co-occurrences	*P*
Aedes cinereus	**0**	**0–2**	**0.004**
Aedes rossicus	**0**	**0–2**	**0.004**
Aedes vexans	132	123–138	0.260
Anopheles claviger	3	5–9	0.422
Anopheles hyrcanus	1	2–5	0.486
***Anopheles maculipennis* s.l.**	5	9–15	0.150
Anopheles plumbeus*	**12**	**41–53**	**< 0.001**
Coquillettidia buxtoni	0	1–3	0.506
Coquillettidia richiardii*	**14**	**33–43**	**< 0.001**
Culex hortensis	1	1–3	0.250
Culex martinii	0	0–1	0.250
Culex modestus	11	15–22	0.250
***Culex pipiens* s.l.**	338	334–341	0.330
Culiseta annulata	13	16–23	0.484
Culiseta longiareolata	2	3–7	0.588
Ochlerotatus annulipes	**0**	**13–19**	**< 0.001**
Ochlerotatus caspius	35	29–38	0.208
Ochlerotatus cataphylla	0	1–2	0.894
Ochlerotatus detritus	**0**	**0–1**	**< 0.001**
Ochlerotatus dorsalis*	**19**	**7–12**	**< 0.001**
Ochlerotatus geniculatus*	**53**	**36–46**	**0.004**
Ochlerotatus pulcritarsis	7	**2–5**	**0.004**
Ochlerotatus pullatus	**0**	**5–9**	**0.012**
Ochlerotatus punctor	0	0–1	0.894
Ochlerotatus sticticus	4	**12–19**	**0.004**
Uranotaenia unguiculata	0	1–3	0.534

To disentangle these potential mechanisms, we applied path analyses, aiming to separate the direct associations between the abundance of *Ae. albopictus* and that of native mosquito species from indirect effects that act through environmental traits. First, we identified those abiotic ecological factors that shape the abundance of *Ae. albopictus*. Specifically, we found that the species was more abundant in more urbanized sites, while there was also a significant interactive effect of temperature and precipitation on abundance. The latter pattern suggests that the positive association with temperature is more emphasized in rainy periods than in dry periods. This can be explained by a mechanism in which, for the enhancing effect of temperature, some optimal levels of water are required to provide suitable conditions for breeding. Similar relationships have been repeatedly shown for the same species in other studies relying on different populations or methodologies (Perrin et al. 2022; Zettle et al. 2022; Garamszegi et al. 2023b). These patterns are consistent

with the known ecology of *Ae. albopictus*, which prefers warm climates, thrives in anthropogenic environments, as it predominantly breeds in artificial containers with breeding conditions depending on precipitation levels, rather than natural water bodies with more permanent water supply (Juliano and Lounibos 2005).

Given that *Ae. albopictus* is apparently responsive to certain environmental conditions, it is plausible that the detected co-occurrence patterns with native mosquitoes are casually driven by the similar or dissimilar ecological requirements of the species being compared. Accordingly, we found that the initially observed negative associations between *Ae. albopictus* and two native species. *An. plumbeus* and *Cq. richiardii*, disappeared when environmental variables were included in the models, and the path analyses revealed no direct relationship between *Ae. albopictus* and these native species. *An. plumbeus* is a native forest-associated mosquito that traditionally breeds in tree holes, but has recently expanded into suburban environments in parts of Europe, utilizing artificial breeding sites, such as tires (Lühken et al. 2023). In Hungary, it has occasionally been recorded from lithotelms and technotelms (Tóth 2004), suggesting a similar trend of local habitat expansion. Its ecological shift toward anthropogenic environments may increase overlap with invasive container-breeders like *Ae. albopictus*, raising the likelihood of competitive encounters. This convergence in habitat use could drive the observed negative association, particularly if both species depend on similar larval resources. However, the results indicate that the detected negative co-occurrence patterns likely reflect contrasting habitat preferences rather than direct interactions. For example, *An. plumbeus* may still predominantly breed in forested habitats in Hungary, while *Ae. albopictus*, is primarily associated with urbanized environments, making them co-occur rarely in the same sampling sites. Furthermore, it is also possible that these species follow different temporal dynamics (as reflected by the effect of detection date), and they have different peak activity periods along the year. Hence, the spatial and temporal segregation between these species is more plausibly explained by environmental filtering than by direct biotic exclusion.

A similar argument can be made for the indirect relationship between *Ae. albopictus* and *Cq. richiardii*. *Cq. richiardii* is a widespread Palearctic mosquito that typically breeds in permanent aquatic habitats rich in emergent vegetation, such as reed beds, lakeshores, marshes, and old riverbeds (Becker et al. 2010). Its larvae are largely sedentary and depend on submerged macrophytes for oxygen uptake. The distinct ecological preferences of *Cq. richiardii*—favoring vegetated, often rural aquatic habitats—contrast with the warm, urban, and container-based environments favored by *Ae. albopictus*. These differences emphasize the role of spatial segregation as a main explanation for the negative co-occurrence pattern between the two species.

The path analyses implied a more direct (positive) relationship between the abundance of *Ae. albopictus* and that of *Oc. dorsalis* and *Oc. geniculatus*. However, it is challenging to find a biological explanation for *Ae. albopictus* favoring large population sizes for these two native mosquitoes. Therefore, we suggest that the casual links between species occur due to some unmeasured environmental variables that would actually mediate the observed causal relationships. It is plausible that, for example, other components of habitat characteristics, additional climatic factors (such as winter temperature, wind) or microhabitat-level interactions, and predation pressure result these species being captured together more frequently than could be expected by chance. Accordingly, *Oc. geniculatus* is known to develop primarily in stable breeding sites such as tree holes in forested areas (Tóth 2004), but it has also been reported from technotelms—artificial containers—similar to those exploited

by *Ae. albopictus*. This occasional overlap in larval habitats may contribute to the observed positive association in trap captures. While our analyses considered several key abiotic and landscape-scale factors, it is likely that other relevant drivers also influence mosquito community composition and it remains plausible that some causal effects were not captured in our statistical models (e.g., note the considerable amount of unexplained variance). It might be that future studies considering other ecological traits will be better at explaining the observed overlap between native and invasive species. Therefore, further research is needed to identify additional environmental factors that may underlie the observed co-occurrence patterns. Furthermore, as traps were positioned in areas where we expected high mosquito activity, such as near water bodies and in urban areas, we can also propose that these non-random aspects of sampling may have contributed to the co-occurrence of species. Accordingly, we cannot exclude that these species were not sampled in the full range of their environmental requirements. It is important to emphasize that our findings are based on correlative analyses, and should therefore be interpreted with caution, particularly regarding potential causal relationships between species. We also emphasize the need for targeted laboratory experiments to explore how specific characteristics of breeding habitats influence competitive interactions among mosquito larvae. We suggest that our correlational field-based findings can provide a valuable foundation for the design of such controlled experiments in the future.

While our study relies on a large, standardized dataset, we acknowledge that BG-Sentinel traps baited with CO_2 and synthetic lure may exhibit species-specific attractiveness, which could affect the catching probabilities of some mosquito taxa. Several studies have reported such biases, showing that trap efficacy can vary substantially across species due to differences in physiology, behavior, or olfactory sensitivity (Roiz et al. 2016; Amos et al. 2020; Lee et al. 2024). These differences can lead to over- or underrepresentation of certain species in trap samples, potentially influencing co-occurrence patterns and inferred associations. Accordingly, our interpretations are made with caution and in consideration of these methodological limitations we acknowledge that the composition of the mosquito community observed within the traps does not necessarily reflect the composition of the mosquito community in the wild. However, the target invasive *Ae. albopictus*, is known to be effectively sampled by this trap type in Hungary (Garamszegi et al. 2023a) and in other countries (Li et al. 2016; Wilke et al. 2019). According to Lühken et al. (2014), the BG-Sentinel trap is probably the best solution for general monitoring or surveillance programs of adult mosquitoes in Central Europe. We recognize that certain native species—particularly those preferring vegetated, shaded, or highly specialized larval habitats—may be under-sampled, especially if their adult females are less attracted to the lure configuration used. Most importantly, we applied the same trap type with identical bait across all sites and years, thereby the selectivity of the BG-Sentinel traps should not raise sampling bias for the hypotheses under test. Therefore, although absolute abundance values may reflect species-specific detection efficiency, comparative patterns across sites and between species pairs should still be robust, provided interpretations are made with caution regarding the composition of the mosquito community. Future studies incorporating multiple trap types, or calibrating species-specific detection probabilities using independent larval surveys, could further refine our understanding of these patterns. In addition, the observed co-occurrence patterns may also be mediated by differences in host-seeking behavior and dispersal capacity across mosquito

species. Because BG-Sentinel traps target host-seeking females, their effectiveness partly depends on the proximity and composition of vertebrate host communities. Species with strong anthropophilic tendencies, such as *Ae. albopictus*, may be more frequently captured near human habitations, while ornithophilic or mammalophilic species might be underrepresented if their preferred hosts are scarce near trap sites. Furthermore, species differ in their ability to disperse from larval habitats to locate hosts, potentially decoupling adult presence from larval coexistence. Therefore, while adult mosquito assemblages offer valuable insights, they may not fully reflect larval-level interactions such as resource competition. This underscores the importance of integrating adult and larval surveillance to better infer ecological mechanisms underlying observed spatial patterns.

Taken together, we have shown that *Ae. albopictus* shows remarkable co-occurrence patterns with several native mosquitoes in Hungary, and that its local abundance can display positive relationships with estimates of the diversity of the endemic mosquito fauna. However, by considering some key ecological factors and by applying a path analysis, we were able to demonstrate – at least for two species – that the detected negative associations are unlikely to reflect direct interaction effects between populations (e.g., competition), and that environmental filtering explains species co-occurrences. These insights emphasize the importance of using environmentally informed models to avoid misattributing ecological effects and to better distinguish environmental associations from potential competitive processes. Our study also highlights that the laboratory results suggesting competition between the larvae of different species do not necessarily translate into population patterns detected in the field for reproducing generations. Overall, our results imply that shared ecological preferences can facilitate long-term coexistence even in the presence of potential competitive interactions. Such dynamics may ultimately promote the establishment and persistence of invasive mosquito species in new habitats, offering important implications for invasion biology and vector surveillance strategies. To better understand the ecological mechanisms behind co-occurrence, future studies should adopt a more comprehensive approach that focuses on a broader range of environmental variables and also integrates species-specific morphological, behavioral, and life-history traits into the analytical framework. Such integrative models would help to disentangle the relative importance of environmental filtering, niche differentiation, and biotic interactions in structuring mosquito assemblages. Considering the complexity of invasion processes, incorporating these functional attributes may provide critical insights into the mechanisms that facilitate coexistence or promote displacement among native and invasive mosquito species.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

ZS and LZG conceived the main ideas, ZS performed literature review, ZS and LZG designed methodology for sampling, ZS, GM, NG, ZK collected the data, ZS performed mosquito identification, LZG analyzed the data, ZS and LZG wrote the first draft of the manuscript. All authors contributed critically to subsequent versions and gave final approval for publication.

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Data availability

All of the data that support the findings of this study are available in the main text.

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Supplementary material 1

Basic data forming the basis of the analysis

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Data type: xlsx

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